PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Organisation of the Fossil Plants of the Coal-Measures. Part XIV. The True Fructification of Calamites

William Crawford Williamson

Phil. Trans. R. Soc. Lond. B 1888 **179**, 47-57
doi: 10.1098/rstb.1888.0002

II. *On the Organisation of the Fossil Plants of the Coal-Measures.*—Part XIV. *The true Fructification of* Calamites.

By WILLIAM CRAWFORD WILLIAMSON, *LL.D., F.R.S., Professor of Botany in the Owens College and in the Victoria University.*

Received May 17,—Read June 16, 1887.

[PLATES 8–11.]

THE systematic affinities of the Carboniferous *Calamites* have now been a moot question for close upon fifty years—the period that has elapsed since 1828, when, in his 'Prodrome d'une Histoire des Végétaux Fossiles,' ADOLPHE BRONGNIART first suggested their relationships to the recent Equisetums. At this time nothing was known of examples of *Calamites* encased in a thick vascular cylinder; a product of the exogenous mode of growth resulting from the action of a cambial ring. At a later period BRONGNIART obtained such examples from Autun and elsewhere. But having then a conviction that no Cryptogamic stem could undergo an exogenous development, he concluded that two classes of plants had been comprehended in the genus *Calamites;* the one Equisetiform, to which he continued to give the old name, the other a Gymnospermous type, to which he assigned the name of *Calamodendron.* His well-merited influence led to a wide-spread acceptance of these views; but their correctness began to be seriously questioned many years ago, on morphological grounds.

After a prolonged conflict the conclusions of those who insisted upon the Cryptogamic character alike of *Calamites* and of *Calamodendron* have met with an extensive, though not universal, acceptance. Meanwhile both the opposing schools of Palæontologists recognise the importance of discovering the fructification of these plants. Mr. CARRUTHERS believed that he had found it in examples of *Calamostachys Binneyana*,* and Mr. BINNEY arrived at a similar conclusion.† I have always rejected these conclusions, because of the conspicuous differences between the morphology of the Calamitean twig and that of the axis of the *Calamostachys.* These differences appeared to me much too great to make it possible for the one ever to have been a prolongation of the other.

In 1869 I published in the 'Memoirs of the Literary and Philosophical Society of

* 'Journal of Botany,' December, 1867.

† 'Palæontographical Society,' volume for 1867.

6.2.88.

Manchester'* a memoir "On a new form of Calamitean Strobilus from the Lancashire Coal-measures." The specimen described was found by Mr. BUTTERWORTH in a nodule from the Upper-foot coal in Strinesdale, near Saddleworth, in Lancashire. It was but a fragment, consisting of three nodes and two intermediate internodes. Its basal and terminal nodes were alike wanting. The portion in our possession belonged rather to the lower than the upper part of the strobilus. Though but a fragment, its well-preserved internal organisation sufficed to show the general features of the strobilus, which differed widely from those of any Carboniferous fructification previously observed.

I ventured to construct a restored diagram of this strobilus,† and also pointed out a peculiar arched arrangement of the vessels of the xylem at each node, which I had hitherto seen only in the true *Calamites*. This fact, combined with other structural peculiarities equally Calamitean, led me to conclude that the strobilus was not only the fruit of a highly developed form of *Calamites*, but that it was the only one hitherto discovered which had any claim to that position.‡

Seventeen years elapsed before further traces of this fruit were discovered. But a few weeks ago Mr. JAMES LOMAX, of Ratcliffe, one of that small band of auxiliaries to whose diligence as collectors I have long been indebted for many of the materials upon which my researches have been carried on, brought me some new sections made from a nodule given to him by another of my assistants, ISAAC EARNSHAW, of Oldham. To my delight I found in these sections several specimens of the long-wished-for strobilus. What remained of the nodule was subsequently cut in such directions as promised to afford the best results. We have now not only much additional knowledge respecting the structure of the strobilus, but the clearest proofs that I was not mistaken in 1869 when I expressed my strong conviction that it was the true fruit of *Calamites*. The most absolute of these proofs is seen in the fact that each of three of these newly-discovered strobili had its basal peduncle attached to it; and that these peduncles are ordinary Calamitean twigs of the type to which our French friends have long assigned the generic name of *Arthropitus*, and which they have, until recently, regarded as a Gymnospermous genus.

The sections represented in the plates have been made in as many directions as our specimens admitted of; the only way in which their complicated structures could be resolved.

Like the *Calamites*, each strobilus has a fistular medulla. The fistular cavity, marked *a* in each figure displaying it, is surrounded by a thin medulla, *b*. In the transverse

* Third series, vol. 4.

† *Loc. cit.*, Plate 8, fig. 13.

‡ See also the First Edition of BENNETT and VINES' translation of SACHS' 'Text Book of Botany,' p. 377, where, by some oversight, the strobilus is referred to under the name of *Volkmannia Dawsoni*, which is a very different plant. The error was corrected on p. 408 of the Second Edition of the same work.

sections, figs. 1, 2, 3, and 4, (Plates 8, 9), this tissue resembles a very regular parenchyma, the cells of which are largest near the periphery of the fistular cavity. In the longitudinal sections they are seen to be very variable in size and form. This variability is well seen in fig. 6, *b*, where nearly every cell is accurately delineated; and in fig. 5 their general character is represented as correctly as the size of the figure admitted of. Many of these cells have rectangular transverse septa; in others these septa are oblique and overlapping. The latter form especially prevails in fig. 5. These medullary cells are usually most elongated vertically in the internodes, becoming much shorter, and their arrangement much less linear, at each node.

The peripheral limit of this medulla may be regarded as marked, in transverse sections, by a circle of longitudinal canals, which are constant as to number throughout the entire length of the axis of each individual strobilus. In one example their number is 16; in each of four others it is 18; and in a sixth it is 20. These canals are unquestionably identical with the internodal canals of the ordinary *Calamites*, from which, as seen in the peduncles of the strobili they present no differences whatever; but within the strobili themselves, especially at the nodes, we find these canals arranged in pairs, as seen at *c*, *c*, in figs. 1, 2, and 4. This apparent dual arrangement is produced by a peculiar segmentation of the axis at and near each node, yet to be described. The canals have a mean diameter of about $\frac{1}{400}$ (·0025) of an inch; one of them is seen at *c* in the long radial section, fig. 6 (Plate 11); and they also appear more interruptedly at the points *c*, *c*, of fig. 5 (Plate 10).

The tissues which closely invest these canals are dense and their elements minute; they consist, on the medullary side, of small cells; but transverse sections reveal, on the cortical side of each canal, a wedge-shaped bundle of small vessels or tracheids, fig. 2, *d*. Each wedge is composed of several longitudinal vascular laminæ, which, starting from a canal, diverge somewhat as they proceed outwards, thus giving to each bundle the wedge-shaped contour seen in transverse sections of young *Calamites*. The larger medullary cells, already referred to, extend outwards between each pair of the canals and their vascular bundles (fig. 4, *b′*); these cells represent the primary medullary rays of the ordinary *Calamites*.

In Plate 11, fig. 6, *d*, some of the vessels of one of these wedges are seen outside the canal, *c*. Their number increases at *d′* as they approach the node, *f*, where the continuity of the individual vessels is interrupted; a result either due to a disturbance of their parallelism, or, what is also probable, some of them may resolve themselves into shorter tracheids. Whichever may be the case, these vessels or tracheids arch over the node, as they have long been observed to do in the *Calamites*. This arrangement is due to the circumstance that the first-formed of these vessels or tracheids were very short, not extending beyond each node into the adjoining internodes; the additions made exogenously to the exterior of those previously formed became successively more and more elongated; hence they described a series of arches, each arch enclosing the smaller one upon which it rested, whilst its two extremities encroached increasingly

upon the internodes, d'' and d'', above and below the node. This arrangement, which first suggested to me the idea that these strobili must be Calamitean, is also seen in Plate 10, fig. 5, d', d'. At the several points, b', b', of the latter figure these vessels are wanting, the section having passed, at these points, between two vascular wedges, *i.e.*, in the radial planes of primary medullary rays.*

The vessels composing these bundles are small, their mean diameter being less than $\frac{1}{800}$ (·00125) of an inch. Their structure is not well preserved in these strobili; but enough remains to show that, whilst some of them are reticulated (Plate 8, fig. 7), others are barred (fig. 8); amongst the latter we find some of the type so characteristic of the *Calamites*, in which the fissures, representing the bordered pits of the common scalariform vessel, are so enlarged vertically as to assume an oval form (Plate 9, fig. 9).

The Cortex.—At each internode this is an extremely thin cellular layer outside the ring of vascular wedges; but where the broad primary medullary rays separate those wedges there is no distinct line of separation between the cells of the cortex and those of the medulla (Plate 10, fig. 5, b', b'). At each node the cortex expands into a cellular lenticular disk. This is an organ of considerable thickness at its centre, but becomes rapidly thinner peripherally. At its outer margin it subdivides into a number of free bracts, which curve upwards, investing the sporangia occupying each internode, whilst their tips rest upon the bases of the bracts of the next superior nodal disk (Plate 10, fig. 10, k, k). The greater portion of the thick central part of this disk lies, as is shown in Plate 10, fig. 5, h, h', h'', and Plate 11, fig. 6, h, h', not on the plane of the node, but a little above it, whilst its gradually contracted vertical extensions in opposite directions invest a considerable portion of each internode above and below the central plane of the disk. In its thicker portions this organ is composed of a mass of coarse parenchymatous cells, intermingled with prosenchymatous ones (Plate 10, fig. 10, h, h', h'', fig. 5, h, h', and h'', and Plate 11, fig. 6, h). As it extends outwards from the central axis of the strobilus, this disk first bends downwards, but soon returns upwards with a bold curve, where its bracts, as already stated, enclose the entire internode. Its thinner peripheral portions are chiefly composed of prosenchymatous cells (Plate 11, fig. 6, h').

A verticil of long slender sporangiophores springs from the upper surface of this disk, free, though not far, from the central axis of the strobilus. The base of one of these is seen at fig. 5, l, and a similar one at fig. 10, l; whilst at l' of the latter figure the entire length of one of these organs is preserved. In my memoir of 1868 I attempted a restoration (*loc. cit.*, fig. 13) of this strobilus, in which the only feature of importance requiring correction is the direction given to this sporangiophore. Having then only discovered its basal portion (*loc. cit.*, fig. 6), I made it ascend into the internodal area

* In describing these xylem structures, I have employed the alternative expressions, vessels or tracheids, because, in these fossil plants, it is absolutely impossible to determine with which of these elements we are dealing.

too perpendicularly, instead of bending its ascending portion obliquely outwards as well as upwards.

The above illustrations of vertical sections of these strobili render an understanding of the transverse and oblique ones easy. Plate 11, fig. 11, is a transverse section, enlarged 36 diameters, of a peduncle of a strobilus. In one of my specimens this peduncle was sufficiently long to furnish four such sections. All the specimens I have seen have exactly the same structure, only varying slightly in the number of the vascular wedges and internodal canals. We have a fistular medullary cavity at *a*, which is constricted, but not subdivided by diaphragms at the several nodes; the medullary cells invest this cavity at *b*. A verticil of internodal canals is seen at *c*, each canal having in close contact with its outer side the vascular wedge, *d*. Intermediate between each two canals and their associated wedges we have the primary medullary rays, *b'*. Each of these features is absolutely identical with what we find in a young Calamite of the Arthropitan type. The diameters of these peduncles range between $\frac{1}{9}$ (·11) and rather more than $\frac{1}{12}$ (·16) of an inch. As is so commonly the case with ordinary Calamites, every one of them is decorticated. Plate 8, fig. 4, represents a transverse section made in a plane a little below that of the greatest diameter of a nodal disk. Its medullary cavity, *a*, medullary parenchyma, *b*, and internodal canals, *c*, do not differ materially from the same structures as seen in the sections of the peduncle; but externally to these structures we now discover an enlarged cortical zone, *e*, in which we find nine large vertical lacunæ, *i*, each having an oval section. These lacunæ can scarcely fail to remind us of those which occupy a similar position in the cortex of the living Equisetum. The two differ in one respect. In the living plant we have one such cortical lacuna between each two of the internodal canals (the *carinal* canals of SACHS). But in the fossil strobilus we find one cortical lacuna between every alternate *pair* of internodal canals. Plate 8, fig. 2, represents a transverse section through the sporange-bearing portion of a strobilus, made near the middle of an internode, at which point the intersected axis, *a*, *b*, *c*, *d*, differs but little from the corresponding transverse section of the peduncle, fig. 11. But it is otherwise with figs. 1 and 3, each of which represents a section of which one-half passes through a nodal disk at a higher level than was done in the specimen fig. 4. At *h*, *h*, in each of the figures 1 and 3, where the disk extends peripherally beyond the lacunæ, *i*, it consists of the coarse parenchyma shown in fig. 5, *h*, *h'*, and *h''*, and in fig. 6, *h*.

In the specimen, fig. 1, the section has been made obliquely through the strobilus, having passed through the nodal disk at its lower half, but ascended into the internode above the disk at its upper margin; here we see the cortical lacunæ at *i*, *i*, whilst at *i'*, *i'*, they are only represented by mere concave longitudinal grooves on the exterior of the axis, which grooves become less and less conspicuous as we approach the centre of the internode, as is shown in Plate 8, fig. 2. On each side of the segment, *h''*, of the disk we discover two small cuticular lacunæ, *i''*, *i''*, which we shall

meet with again in figs. 17 and 18. At the outer angle of each of these small lacunæ we find a sporangiophore, l', intersected transversely close to where it sprang from the nodal disk. These sporangiophores, along with similar ones near to them, are part of a verticil of twenty, the remaining sixteen of which are seen to recede further and further from the central axis of the section until, at l, l, they become isolated amongst the spores of the internode above the disk from which they spring.

The number of these sporangiophores is invariably identical with that of the internodal canals, c, and of the vascular wedges external to those canals. It is also exactly double that of the *larger* cortical lacunæ, i, of the nodal disk. Transverse sections of these sporangiophores vary somewhat in form; but such sections always approximate to the contour of fig. 12, Plate 10. Apparently they consist only of prosenchymatous cells, disposed longitudinally; but it is scarcely probable that they should not contain a small vascular bundle of some kind. I have, as yet, discovered no trace of any such bundle, either given off by any of the axial vascular wedges, or traversing any one of my numerous sections of the cellular nodal disk.

The Sporangia.—Combining sections made in various directions, as in figs. 2, 3, 13, and 14, I have been enabled to determine the arrangement of these organs. Fig. 2 we have already seen to be a transverse section across an internode. This strobilus seems to have been compressed laterally. The sporangia have been arranged in two concentric verticils, m and m', between which the sporangiophores passed obliquely upwards and outwards.

Plate 9, fig. 3, is an oblique transverse section which has passed through the descending portion of a nodal disk, intersecting the bases, k, of the peripheral bracts at the upper part of the figure; hence it has failed to intersect any of the sporangia. But on its lower half it has almost cut through the strobilus in the plane of the obliquely ascending sporangiophores. At this latter part we again discover the two series of sporangia, m and m', and the sporangiophores at l, l.

Plate 11, fig. 14, represents a yet more oblique section, which passed through two nodal disks, h and h', and three internodes, g, g', and g''. Both g and g' show the two verticils of sporangia at m and m.

Plate 9, fig. 13, represents the only fragment of a true tangential section I have been able to obtain, and this is but an imperfect one, owing to a circumstance yet to be described. In this section the marginal bracts of two nodal disks are intersected at k, k', and the two verticils of sporangiophores ascending from these disks are seen at l, l'. The walls of the sporangia constituting the upper and inner verticil of the internode l' are present at m', and the sporangiophores at l, l.

Several points are demonstrated by the facts just described: the sporangia are very numerous; they are all arranged radially in two verticils; as is shown by fig. 13, m', their vertical length much exceeds their transverse diameters; their perpendicular lateral surfaces are flat and virtually parallel to each other, allowance being made for the fact that, seen in transverse sections, the inner border of each sporangium is somewhat

thinner than its outer one. In the inner verticil this inner border has a mean diameter of from $\frac{1}{150}$ (·0066) to $\frac{1}{50}$ (·02) of an inch, whilst their peripheral margins in the same verticil range between $\frac{1}{80}$ (·012) and $\frac{1}{50}$ (·02) of an inch. In the outer verticil the tangential diameter of each sporangium is rather greater—ranging from $\frac{1}{50}$ (·02) at their inner edges to $\frac{1}{30}$ (·033) of an inch at their peripheral ones. I have sought in vain for evidence showing where and how these sporangia are attached to the sporangiophores. As a rule, each sporangiophore appears to be the point at which four sporangia, two from each verticil, meet, as is the case with the genus *Calamostachys;* but there seem to be exceptions even to this arrangement, apparently due to the number of the sporangia being less constant than that of the sporangiophores. The wall of the sporangium is composed of a single layer of cells (Plate 10, fig. 15, *n*) flattened externally, but projecting convexly into the interior of the sporangium. The cell-walls, especially the inner and lateral ones, are slightly thickened. Each spherical spore (fig. 15, *o*) is enclosed within a ruptured mother-cell, *o′*, and has a small dark mass in its centre, the nature of which is doubtful.

In several of my sections, especially fig. 1, the sporangia are in a noteworthy condition; whilst some of the sporangia retain their sporangial walls, these walls have wholly disappeared from others. Thus in the section, fig. 1, the only traces of them which remain are a few isolated fragments. The same is the case at *m*, in the lower part of the internode *g* of fig. 13. Other sections show smaller portions of sporangia in a similar state. In such examples the sporangiophores are simply surrounded by compact masses of free spores. The only probable explanation of this condition is that these sporangial walls have been removed by a process of absorption or degradation in order to liberate the spores which, unlike those of the living Equisetums, are not provided with other special means of being set free. If this explanation is correct, the masses of spores must have been held together in the later stages of their development solely by the nodal disks and their upturned fringes of broad peripheral bracts.

Fig. 16 represents a lateral view of the lowest node and internode of Mr. BUTTERWORTH's original specimen, from which the section, fig. 1, was taken. I presume that the vertical ridges separated by furrows indicate the contours of a corresponding number of marginal bracts. Fig. 17 represents the concave under surface of the same specimen,* the concentric inflections of which evidently represent those of a nodal disk; most probably those of its inferior surface. In its centre, *a*, we see the fistular medullary cavity. Surrounding this we have at *i* an inner verticil of ten cortical lacunæ, identical with those seen at *i′* of fig. 1. Yet more externally we have twenty smaller lacunæ, *i″*, occupying the same positions as the two indicated by *i″*, *i″*, in fig. 1. The extreme regularity of these latter lacunæ is remarkable; the more so, because of their imperfect preservation in other sections. That they were

* This was obviously not the lowest node of the strobilus.

normal features of the disk is shown by the section, fig. 18, which represents a fragment taken from fig. 17 and further enlarged. The two sets of lacunæ, *i*, *i′*, seen in that figure, are seen in fig. 18 to have well-defined contours suggestive of something more than accidental lesions. They obviously bear some definite relations to the sporangiophores, *l*, of fig. 1, traces of which also appear at *l′*, *l′*, of fig. 18.

Fig. 19 (Plate 9) is a radial section of a small twig or stem of a young Calamite, introduced for comparison with Plate 11, fig. 6. In this Calamite *b* is the medulla; *c*, *c*, internodal canals; *d*, a vascular bundle; and *d′*, the arching vessels of that bundle opposite the node *f*.

Having thus shown most of the details of the organisation of this strobilus from actual specimens, we run little risk of error in representing its morphology as seen in a vertical section by the restored diagram, fig. 20 (Plate 9). The letters of reference are used in the same way as in the previous figures. The sections at *m′*, *m′*, show the inner and outer verticils of the sporangia only, having passed between two sporangiophores whilst at *l*, *l*, these sporangiophores are intersected vertically. The cortical lacunæ introduced at *i*, *i*, are omitted elsewhere for the same reasons.

The fact that so many specimens of these fruits, otherwise so rare, were aggregated in one small nodule probably indicates that they were borne singly upon the extremities of several small branches clustered round the extremity of one stem.

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Plate.	Fig.		Pages on which references are made to the figures.
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All the above references to the "Cabinet" indicate that each specimen so referred to will be found in my cabinet under the number assigned to it in the text. This cabinet will finally be placed in the Botanical Department of the Museum of the Owens College, where future students of Palæo-Botany will have free access to it. Whether such observers confirm my views or otherwise, they will have no difficulty in examining for themselves nearly all the specimens upon which those views have been based.

Fig. 1.

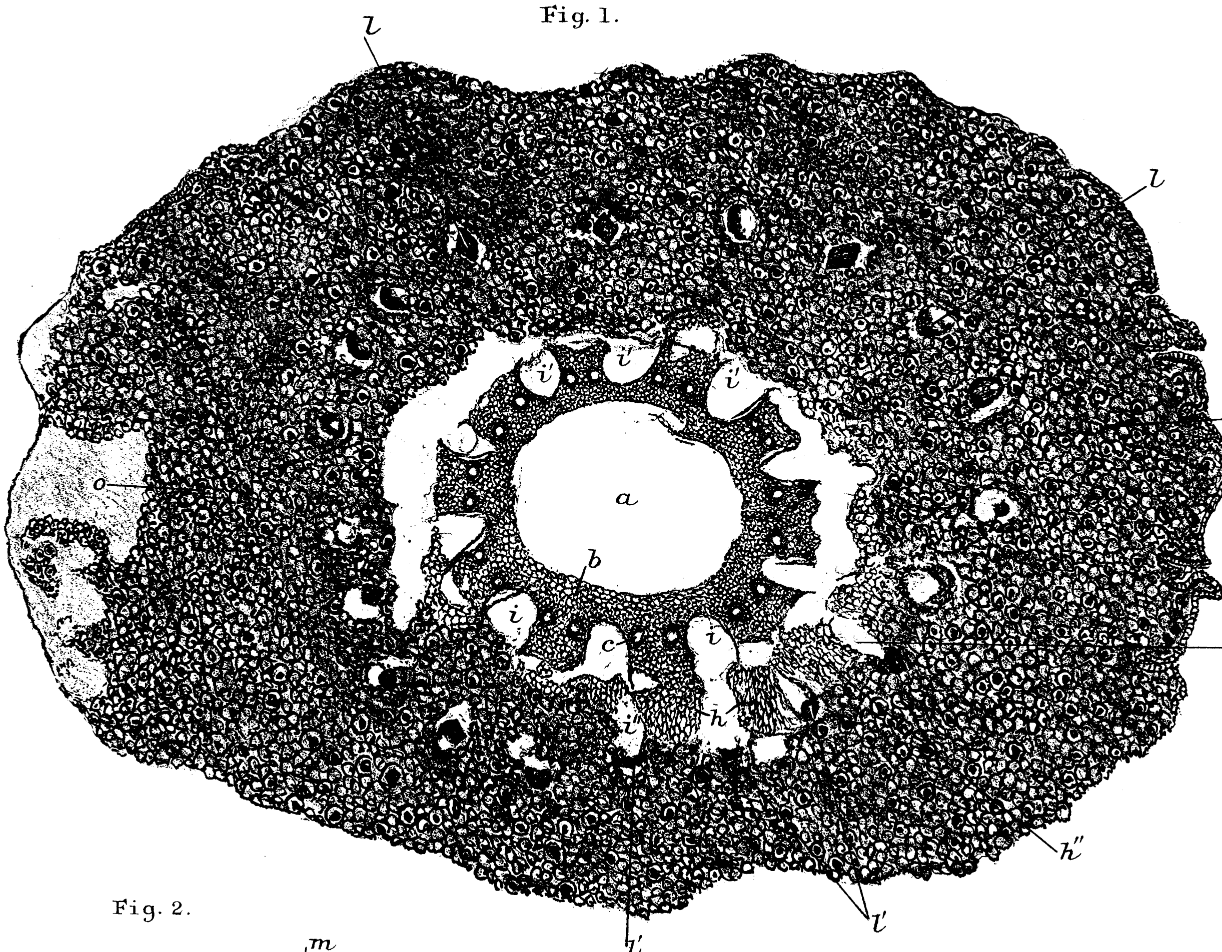


Fig. 2.

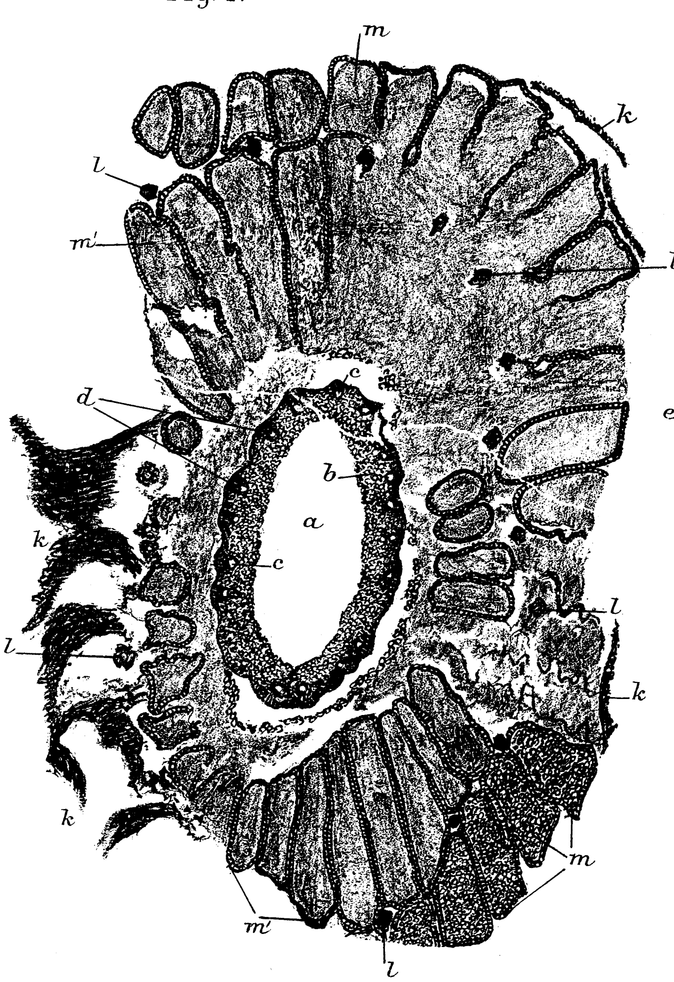
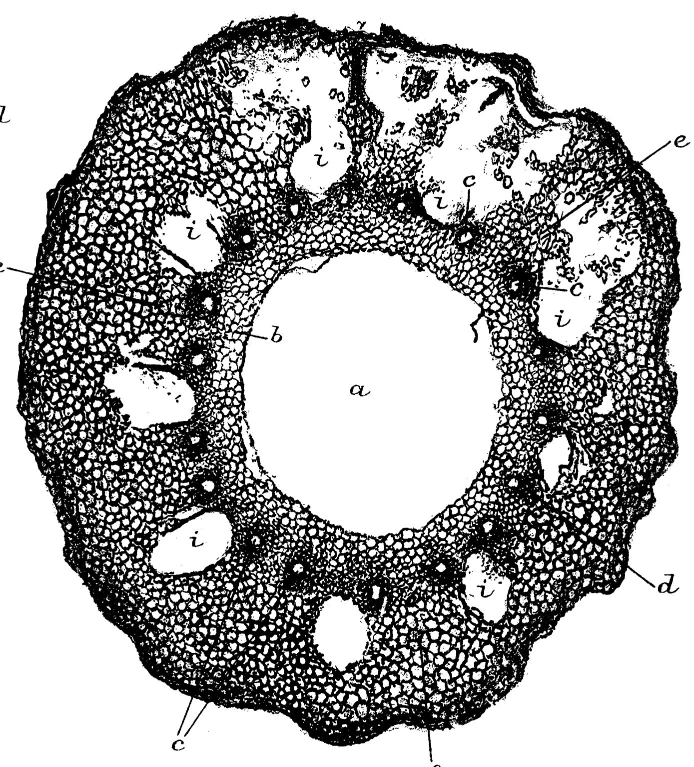


Fig. 4.



C. Williamson, Del.

Whiteman & Bass, Photo-Litho. London.

Fig. 3.

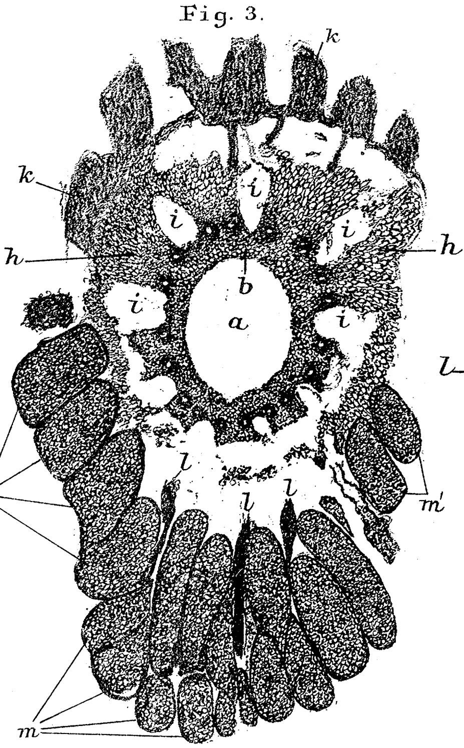


Fig. 20.

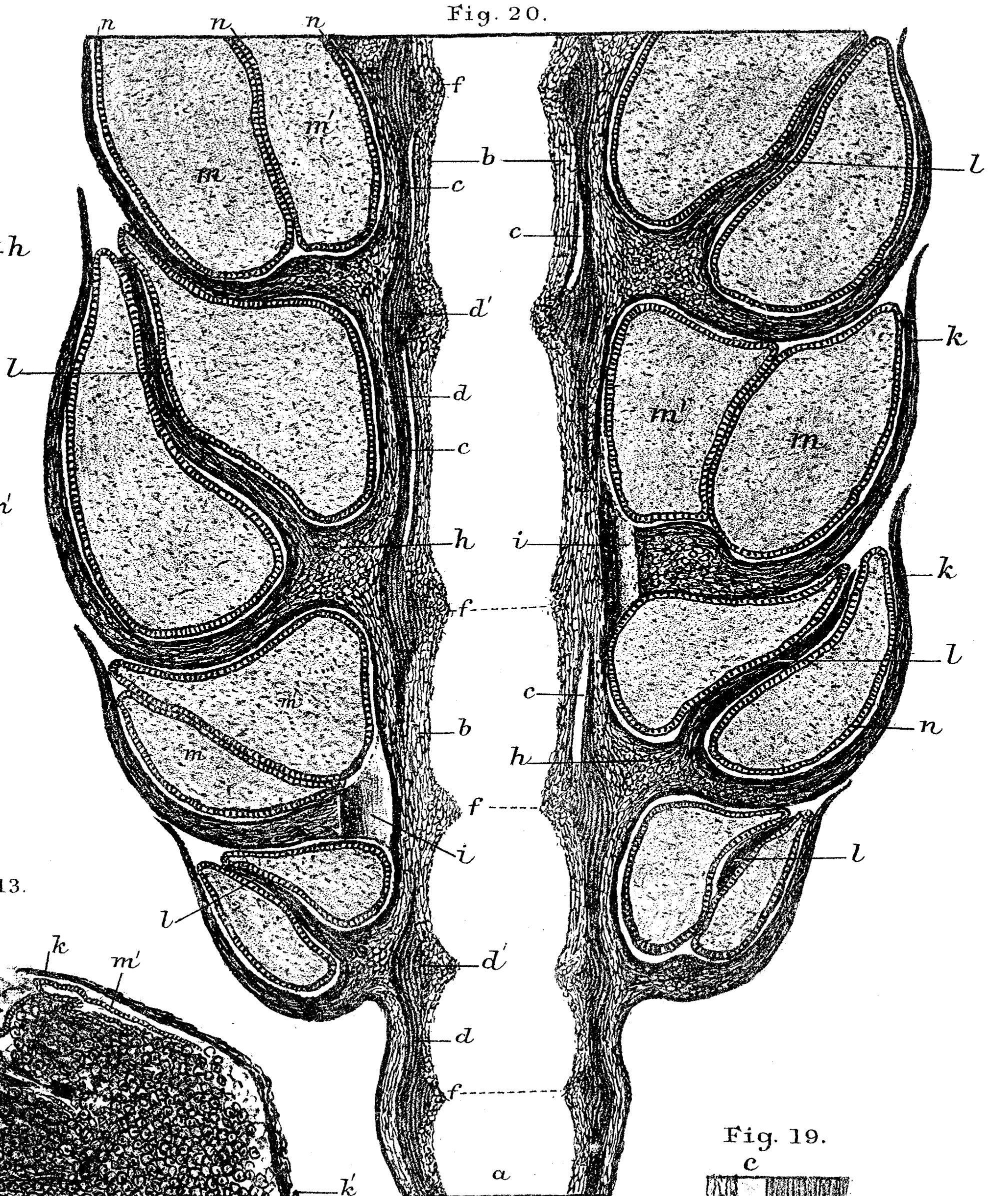


Fig. 13.

Fig. 8.

Fig. 7.

Fig. 9.

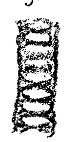
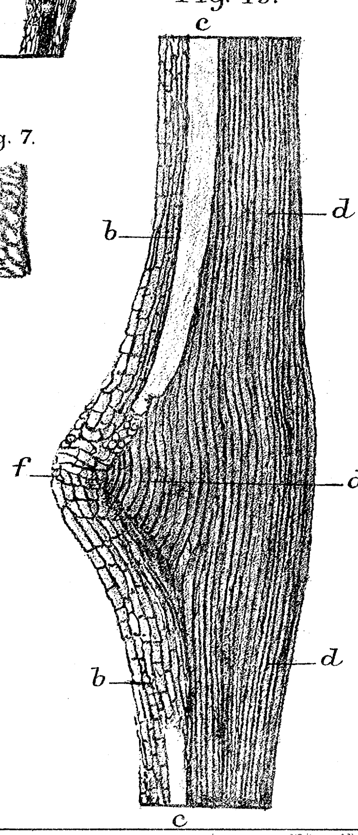


Fig. 19.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Fig. 16.

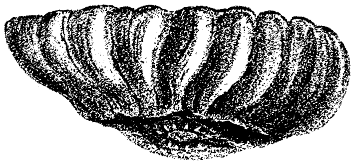


Fig. 17.

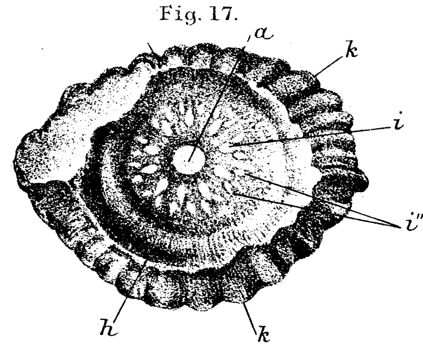


Fig. 5.

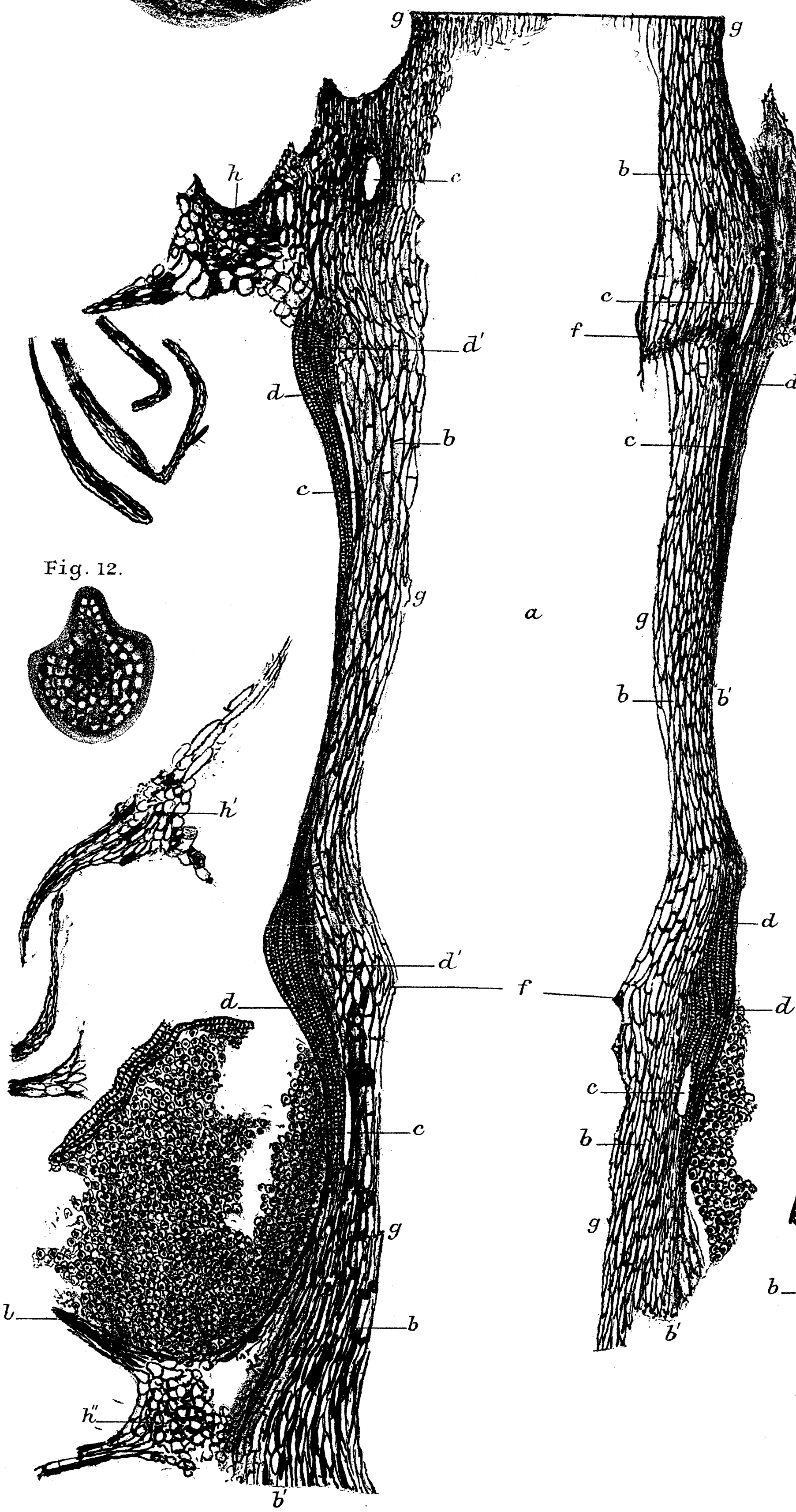


Fig. 15.

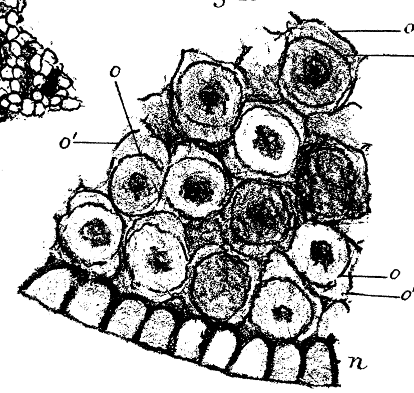


Fig. 12.

Fig. 10.

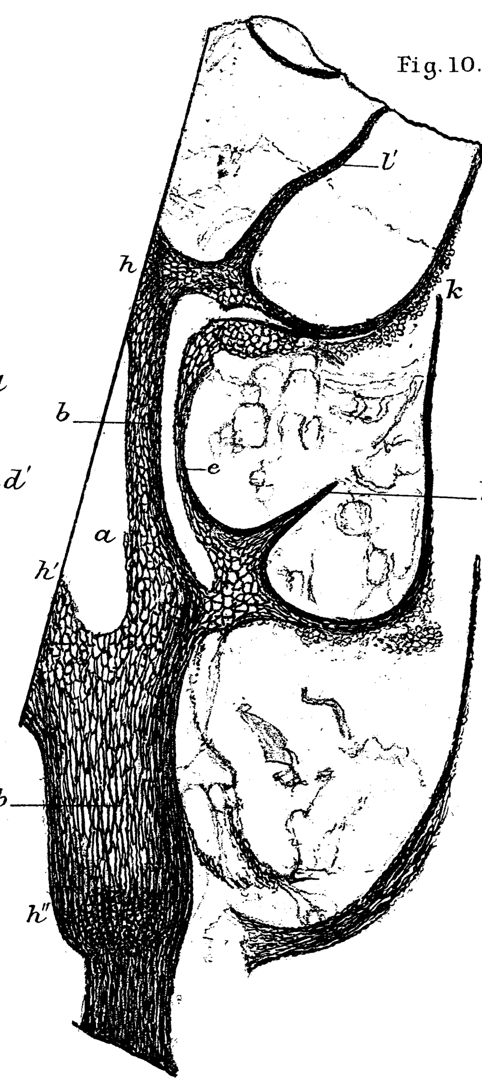


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Fig. 14.

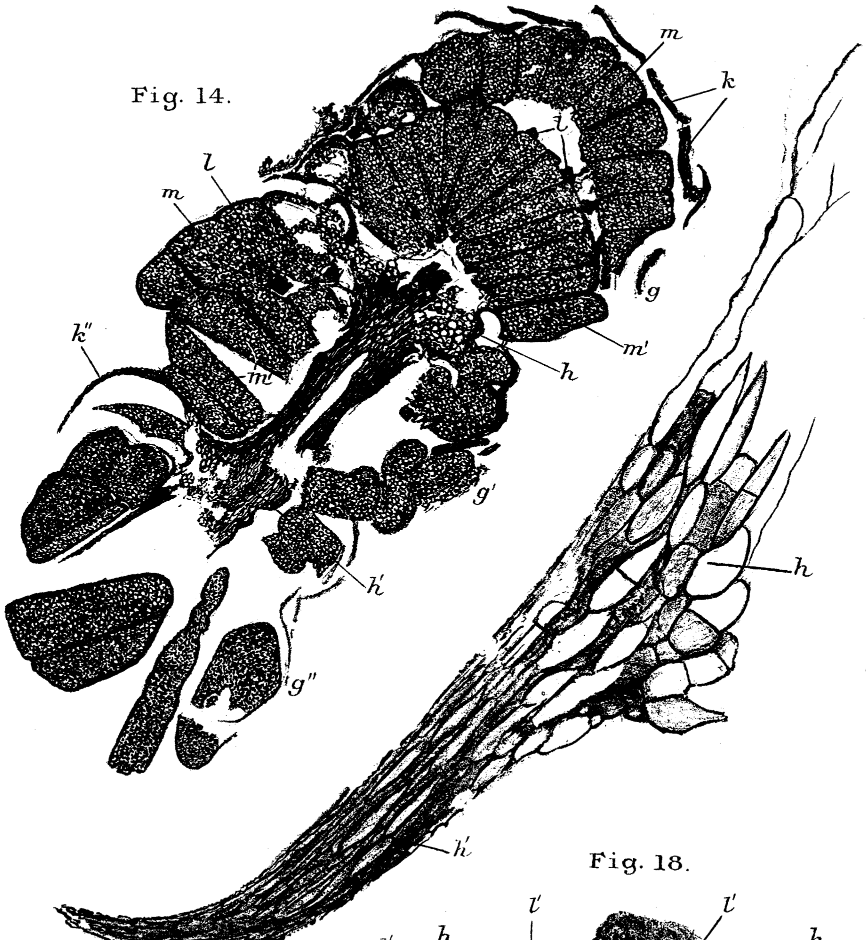

Fig. 6.

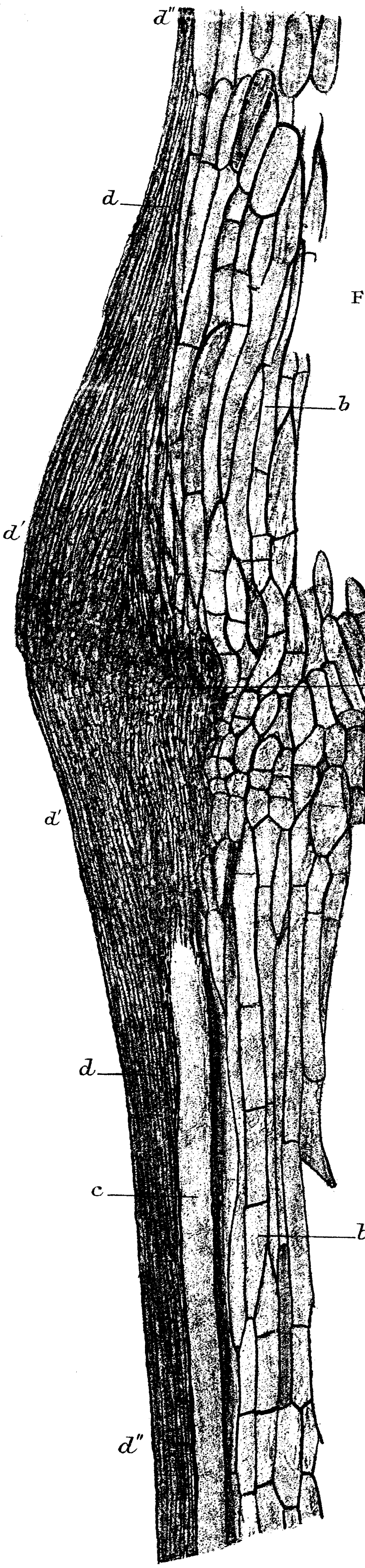

Fig. 18.

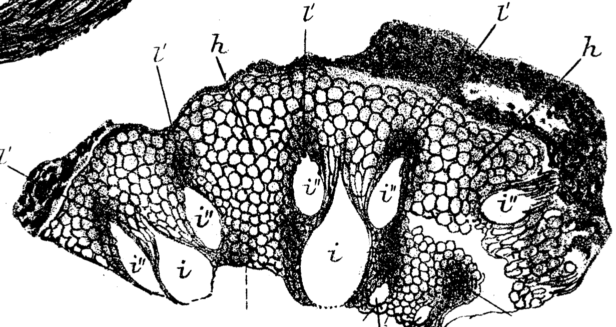

Fig. 11.